

FOOD PRODUCTION AND COMPETITOR DENSITY AS THE
DETERMINANTS OF FEEDING TERRITORY SIZE

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The role of territorial behavior in the regulation of population density has been the subject of extensive theoretical and empirical investigations (e.g., Brown 1969a, 1969b; Fretwell and Lucas 1969; Watson and Moss 1970; Maynard Smith 1974). Although such studies examine the idea that an upper limit may exist to the number of territories which can be packed into any given habitat, few general discussions have considered factors that determine the size of the individual territory. Schoener (1968) explained the positive correlation between feeding-territory size and body size of birds as a response, in part, to decreasing prey density with increasing metabolic requirements. His later model proposed that the size of the territory reflects an equilibrium between the invasion rate of competitors and the expulsion rate of the territory occupant (Schoener 1971). More recently, Covich (1976) and Dill (1978) have investigated additional theoretical determinants of optimal territory size.

The purpose of this paper is four-fold: (i) to develop a general model of feeding territoriality that relates territory size to food production and competitor density; (ii) to partly evaluate predictions from this model with available field evidence; (iii) to suggest additional experimental methods for testing the model; and (iv) to discuss several other environmental effects on territory size.

For this model, feeding territoriality is defined as the nearly exclusive access to and utilization of food resources within a mobile animal's home range as a direct result of that animal's aggressive and/or ritualized expulsion of individual food competitors. Note that although the primary object of territorial defense may be a shelter, a mating site, etc., the resulting restriction in the animal's range may secondarily require defense of a food supply. As long as the space required for maintenance of a food supply is larger than that required for other resources, territory size should reflect the status of factors affecting the food supply. For example, the damselfish *Eupomacentrus planifrons* may simultaneously defend different sized territories in securing different resources, yet the largest of these

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apparently secures a food supply (Myrberg and Thresher 1974) and does vary in size with food production (Thresher 1977).

Regardless of any simultaneous adaptive significance of territorial behavior, a feeding territory is self-evident when the food organisms are sessile or extremely limited in their movements, and the territory is permanent (i.e., continuously defended) and identical in size to the home range (i.e., the animal very rarely, if ever, leaves its territory). The primary field evidence presented in this paper was chosen on the basis of these criteria. Although the model was originally derived from ideas concerning reef fishes, the predictions should be applicable to any species exhibiting feeding territoriality as defined. Examples of such species are discussed below.

NATURAL SELECTION AND TERRITORY SIZE

Any realistic model of feeding territoriality must consider the influence of natural selection upon territory size relative to the bioenergetic components of fitness. The first convincing theory of the evolution of territoriality predicted that this behavior would develop only when the limiting resources in a competitive situation are "economically defensible" (Brown 1964). Thus, selection can favor permanent feeding territories only when the benefits gained through the resulting exclusive access to food resources outweigh the costs due to defensive behavior, i.e., when a long-term net energy gain is established. (Food and energy are here equated. Although factors such as the chemical composition of food are obviously very important characteristics, energy is considered to be the primary component of food value.)

Given that natural selection operates by differential reproductive success, the extent to which a territory occupant will adaptively increase its daily net energy gain depends upon the limit to which additional energy input contributes to reproductive output. Schoener (1971) has broadly characterized animals as being either feeding-"time minimizers" or food-"energy maximizers." Time minimizers exhibit fixed daily energy requirements, since excess energy intake does not increase their potential reproductive success. Such animals may thus minimize their feeding periods and so allow time for more adaptive activities. Schoener (1971) generally considered animals with relatively fixed reproductive outputs, and males more often than females, as being time minimizers.

Food-energy maximizers are animals whose potential reproductive success is directly correlated with their daily net energy gain. Schoener (1971) generally characterized females as being energy maximizers, although sexual selection within territorial systems may result in growing males maximizing their energy input for earlier attainment of social dominance (see Trivers 1972). Moreover, any size individual of either sex may act as an energy maximizer to some extent when excess food energy can be physiologically stored for later use (see Pianka 1976).

While it appears that the distinction between time minimizers and energy maximizers may define the opposite ends of a theoretical spectrum of optimal feeding behaviors, the terms themselves are somewhat misleading. Within certain constraints, selection will favor any animal that maximizes the amount of energy it

obtains per unit foraging time. Thus, an energy maximizer that became satiated each day would be functionally identical to a time minimizer. In practice, then, the primary difference between these foraging types may be the relative proportion of time each spends feeding. For lack of better terms, however, the original dichotomy proposed by Schoener (1971) will be retained.

In the following optimization model, then, a true feeding-time minimizer defends an area just large enough in the long run to provide sufficient food to satisfy some fixed daily energy requirement. Such behavior allows a maximum amount of "spare" time per day, which for a nonbreeding animal may be spent watching for competitors and/or predators, as well as simply resting. A food-energy maximizer, on the other hand, ideally defends an area providing a long-term maximum net energy gain. It will be shown that such behavior secondarily minimizes spare time. Thus, the relative proportion of time nonbreeding animals spend feeding may provide operational criteria for distinguishing these foraging strategies (see below).

The specific goal of the model, therefore, is to qualitatively predict adjustments in feeding-territory size for time minimizers and energy maximizers in response to variable food production and competitor density. As with any such optimization model, the basic assumption is not that animals behave "optimally" per se, since unsuspected selection pressures may preclude the appearance of a predicted optimum in nature. However, such models can predict in what direction a behavioral response will occur following some known environmental variation.

THE MODEL

In its basic form, the model considers noncontiguous feeding territories maintained during nonbreeding seasons. As discussed below, the relative simplicity of such a system provides an opportunity to adequately test the predictions of the model. The complicating effects of territory contiguity, reproductive activities, and other factors will be discussed in separate sections. The present model does not, however, consider the risk of predation to be a significant determinant of territory size (see Covich 1976 for such considerations).

For simplicity, the model considers the shape of the territory to be ideally circular, with the radius (r) being used as the index of size. For easy reference, the symbols presented in the following development are listed and defined in Appendix A.

Time Budget

The daily time budget of the diurnal territory occupant between breeding seasons is divided into three components:

$$T_{\text{tot}} = T_f + T_c + T_s \quad (1)$$

where T_{tot} is one daylight period. The daily time spent feeding is T_f , while T_c is the daily time spent chasing intruders. The amount of "spare" time available per day is T_s , considered to be "sitting" time for nonbreeding animals.

Competitors

It is assumed that the occupant can survey the entire territory from any point within. Thus, the model may not be applicable to many predatory birds and mammals, which often maintain large territories in structurally complex environments. Indeed, territory size for such animals often does not vary in response to changes in prey abundance (Brown and Watson 1964; Lockie 1966; Southern and Lowe 1968). It is possible that these animals defend food reserves for periods of prey scarcity (Lockie 1966), and may thus function to some extent as "area maximizers" (discussed below).

Assuming the occupant chases (or ritually escorts) each foraging intruder to the territory border, the rectilinear chase distance will vary between 0 and $2r$, with a mean value of r . The mean amounts of time and energy spent expelling one intruder are thus represented by the expressions rt and re , respectively, where t is the time spent and e is the energy consumed per unit chase distance.

The relevant territory intruders are potential food competitors (hereafter simply called "competitors"), which may be either conspecific individuals or members of another species, and may be either territorial or wandering (reviews by Orians and Willson 1964; Myrberg and Thresher 1974). For simplicity, the nonterritorial competitors are assumed to be more or less evenly distributed as they forage. Under these conditions the number of intruders of any given species entering the territory per day roughly equals the product of their density (C), the mean speed at which they wander (s), the diameter of the territory ($2r$), and one daylight period (T_{tot}). This product will not exactly equal the intrusion rate due to various behavioral factors, such as certain competitors learning to avoid the territory.

Of the various species entering the territory, each constitutes a different competitive threat to the occupant. Depending upon the small-scale distribution of the food items, the lower the level of dietary overlap between any given species and the territory occupant, the greater the probability will be that an intruder of that species will pass through the territory without actively foraging. As a rough approximation, then, it is assumed that the percentage of intruders which are chased from the territory varies directly with the percent dietary overlap (o) between the intruding species and the territory occupant. Field evidence indicates that this approximation may be valid for at least two species of territorial reef fish (Ebersole 1977; Hixon 1979).

Given these assumptions, the amount of time required per day for the territory occupant to expel all foraging intruders of n competitor species (T_c) equals the mean temporal cost of chasing one intruder (rt) times the daily number of foraging intruders of each species ($2rT_{\text{tot}}sCo$). Therefore

$$T_c = 2r^2tT_{\text{tot}} \sum_{i=1}^n (sCo)_i. \quad (2a)$$

Similarly, amount of energy required per day to chase all foraging intruders is

$$E_c = 2r^2eT_{\text{tot}} \sum_{i=1}^n (sCo)_i. \quad (2b)$$

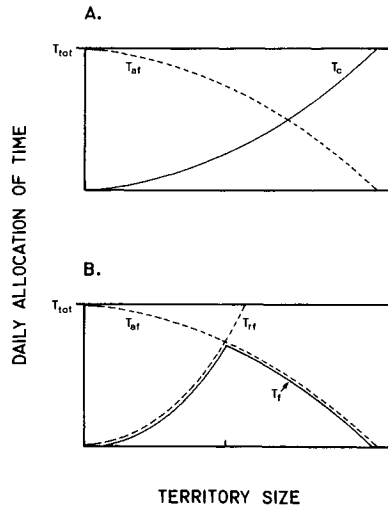


FIG. 1.—A, Total daily chasing time (T_c of eq. [2a]) as a function of territory size (r). The inverse curve (T_{af}) represents the theoretical maximum available feeding time per day, such that the sum of T_c and T_{af} is one daylight period (T_{tot}). B, Time required to consume total daily food production of the territory (T_{rf} of eq. [3b]) superimposed on T_{af} , both as functions of r . The solid line represents the actual daily feeding time (T_f). Below a certain territory size (r') T_f will equal T_{rf} ; at larger sizes T_f will equal T_{af} . See text.

Figure 1A depicts the required daily defense time (T_c) as a function of r . Considering equation (1), if T_c is subtracted from the total daily time (T_{tot}), one obtains an inverse curve ideally representing the maximum amount of time available per day for feeding (T_{af} in fig. 1A). I now consider how much of this available feeding time is actually utilized.

Food

It is assumed that the food organisms in the immediate area of the territory are uniformly distributed, continuously renewing, and essentially immobile. Brown (1964) and Horn (1968) have convincingly developed the idea that such conditions may be necessary for the resources to be economically defensible. Note that these conditions do not preclude environmental heterogeneity. The assumption is simply that, given a change in territory size, the area that is gained or lost will have the same average productivity as the remainder of the territory. Although any given territory is assumed to occupy a single more or less uniform patch, different territories can occupy different patches, and thus vary in overall quality. It is further assumed that the food is immediately consumed and is not transported to a refuge or other central location (see Dill 1978 for such considerations).

Since the territory is permanent, the food must be consumed at some sustainable yield. Field evidence suggests that territorial damselfishes, for example, maintain relatively high standing crops of their algal food (Vine 1974; Brawley and Adey

1977), and that such stocks constitute a maximum sustainable yield (Syrop 1974). It seems likely that selection would favor any permanent territory occupant maintaining a maximum sustainable yield, since this would allow the maximum long term energy gain per unit defended area.

Under these conditions, and if time permits, the occupant will be able to obtain the total amount of available food energy produced within the territory per day ($E_{f\max}$), which will obviously vary with the area of territory (πr^2). Therefore

$$E_{f\max} = \pi r^2 F y, \quad (3a)$$

where F is the daily food production in terms of available biomass produced per unit area and y is the net energy yield per unit biomass of food eaten. The amount of time required to consume this total daily food production (T_{rf}) is thus

$$T_{rf} = \frac{\pi r^2 F}{f}, \quad (3b)$$

where f is the food consumption rate in terms of biomass eaten per unit foraging time.

Note that, assuming the animal is unsatiated and the food is available, the term f can be generally derived from two time components involved in the consumption of a given mass of food: search time, which usually varies with prey density or production, and handling time, which is more or less constant (see Holling 1965). It is assumed that search time is relatively negligible for territorial animals, due to the immobility of the food organisms and the familiarity of the occupant with the microhabitats of the territory. Thus, f is assumed to remain more or less constant.

Figure 1B depicts the available daily feeding time (T_{af} from fig. 1A) with the feeding time required to consume the total daily food production of the territory (T_{rf} from eq. [3b]) as functions of r . The actual amount of time the occupant can spend feeding per day is thus depicted as T_f .

Energy Budget

The daily energy budget of the territory occupant can now be expressed as

$$\Delta E = E_f - E_c, \quad (4a)$$

where E_f is the daily energy gain from feeding and E_c is the daily energy loss from chasing intruders. The quantity ΔE , then, is energy available for metabolic maintenance, storage, growth, gamete production, and sitting, courtship, and other activities; it is obviously maximized by energy maximizers (ΔE_{\max}), but is relatively constant for time minimizers (ΔE_{fix}). In the long run, of course, ΔE must have a positive value for territoriality to persist.

From the preceding development, the amount of energy the territory occupant loses while chasing intruders (E_c) is linearly proportional to the amount of time spent chasing (T_c). Likewise, the amount of energy gained from feeding (E_f) is linearly proportional to the amount of time spent feeding (T_f). Thus the ΔE_{\max} of the energy maximizer can be directly converted to and considered in terms of time

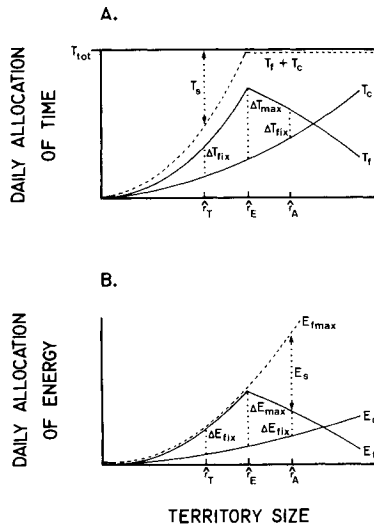


FIG. 2.—A, Total daily chasing time (T_c from fig. 1A) and feeding time (T_f from fig. 1B) as functions of r . The optimal territory size of the time minimizer (\hat{r}_T) occurs at the smallest size such that the ΔT of eq. (4b) equals ΔT_{fix} , thus maximizing daily spare time (T_s). The optimal territory size of the energy maximizer (\hat{r}_E) occurs where ΔT is maximized (ΔT_{max}), while that of the area maximizer (\hat{r}_A) occurs at the largest size where ΔT equals ΔT_{fix} . B, Energy analogs of these time relations. While time minimizers and energy maximizers consume the total daily food production of their territories (E_{fmax} of eq. [3a]), the area maximizer does not, and thus defends food energy reserves (E_s). See text.

(ΔT_{max}). Likewise, the ΔE_{fix} of the time minimizer also has a time analog (ΔT_{fix}), where, in both cases:

$$\Delta T = T_f - T_c. \quad (4b)$$

Note that while ΔE must have a long-term positive value, ΔT might conceivably be negative.

Optimal Territory Size

We are now in a position to determine the optimal feeding territory size. Figure 2A depicts the total daily defense time (T_c from fig. 1A) and feeding time (T_f from fig. 1B) as functions of r . Inserting the fixed time differences (ΔT_{fix}) corresponding to the relatively fixed daily energy requirement of a time minimizer (ΔE_{fix}), we obtain the optimal territory size for such animals (\hat{r}_T). Note that, at \hat{r}_T , the sum of T_f and T_c is less than T_{tot} . The time minimizer thus maximizes its "spare" time per day (T_s in fig. 2A). The maximum daily time differences (ΔT_{max}), which corresponds to the maximum possible daily net energy gain (ΔE_{max}), determines the optimal territory size for the energy maximizer (\hat{r}_E). Note that such animals ideally have no "spare" time. The energetic analogs of these time relations are depicted in figure 2B. (The territory size \hat{r}_A will be discussed below.)

From the derivations presented in Appendix B, the optimal territory size of time minimizers can be expressed as

$$\hat{r}_T = \left[\frac{\Delta T_{\text{fix}}}{(\pi F/f - 2tT_{\text{tot}} \sum_{i=1}^n (sCO)_i)} \right]^{1/2}, \quad (5)$$

and that of energy maximizers as

$$\hat{r}_E = \left[\frac{T_{\text{tot}}}{(\pi F/f + 2tT_{\text{tot}} \sum_{i=1}^n (sCO)_i)} \right]^{1/2}. \quad (6)$$

From these equations, the influence of changes in food production (F) and nonterritorial competitor density (C) upon territory size can be predicted. For the basic model, these predictions are that feeding territory size should (1) vary inversely with food production, but directly with competitor density for feeding-time minimizers, and (2) vary inversely with both food production and competitor density for food-energy maximizers.

The required behavioral mechanisms behind these predictions are not complicated. As depicted in figure 3A, additional time will be required to consume any increased daily food production (see eq. [3b]), so the ascending part of the feeding time curve (T_f) will shift upward. In figure 3B, as competitor density increases, the chasing time curve (T_c) will shift upward due to the increased invasion rate of competitors (see eq. [2a]). In either case the time minimizer merely adjusts the area it defends (\hat{r}_T) to the smallest that provides its fixed daily energy requirement (ΔE_{fix}), which corresponds to ΔT_{fix} . Similarly, the energy maximizer simply adjusts its territory to that area (\hat{r}_E) providing the greatest difference between feeding and chasing time (ΔT_{max}), which corresponds to ΔE_{max} . Thus, the environmental determinants of territory size are mediated through the occupant's daily time budget.

Note that the model assumes that food production and competitor density can vary independently of each other. It is possible, however, that if food production became disproportionately high in a given territory compared with surrounding areas, the competitor intrusion rate might concurrently increase (Brown 1975; Verner 1977; Davies 1978). Where the differences between food patches is not so great, however, this effect would probably be negligible. Although conclusive experimental data on this point is lacking, recent field observations suggest that this effect may be important for certain "area maximizers" (discussed below).

TESTING THE MODEL

Concomitant with the above predicted changes in territory size are changes in the time budget of the occupant (table 1 and fig. 3). These changes provide operational criteria for testing the model without evaluating all the parameters in equations (5) and (6). Baseline time-budget observations, such as those cited below for nectar-feeding birds, can indicate whether the animals being studied are

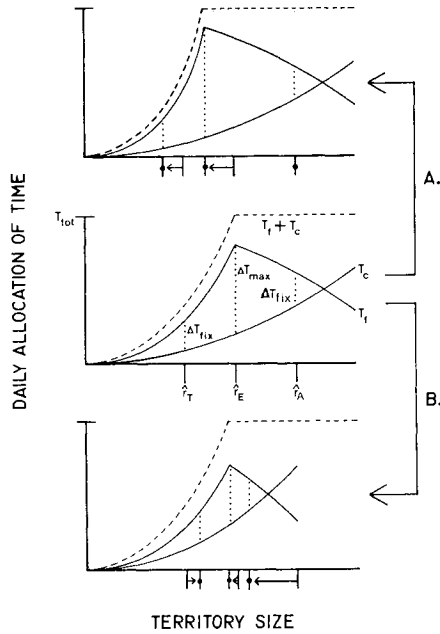


FIG. 3.—Predicted effects of increased food production and nonterritorial competitor density on the optimal territory size. The central graph depicts the hypothetical time relations described in fig. 2, and represents the initial state. The upper and lower graphs depict subsequent changes of the same system and are thus unlabelled. Arrows along the abscissa denote the direction and magnitude of the changes in territory size. A, Increased food production results in decreased territory size for both the time minimizer (\hat{r}_T) and energy maximizer (\hat{r}_E), but does not directly affect the area maximizer (\hat{r}_A). B, Increased nonterritorial competitor density causes an increase in \hat{r}_T , but a decrease in \hat{r}_E and \hat{r}_A . Concomitant changes in time budgeting are listed in table 1. See text.

TABLE 1
PREDICTED CHANGES IN FEEDING-TERRITORY SIZE AND TIME BUDGETING FOLLOWING GIVEN ENVIRONMENTAL VARIATIONS

Forager Type	Territory Size (r)	Feeding Time (T_f)	Defense Time (T_c)	ΔT (= $T_f - T_c$)
Increased food production (F):				
Time minimizer	decrease	decrease	decrease	negligible change*
Energy maximizer	decrease	increase	decrease	increase
Increased competitor density (C):				
Time minimizer	increase	increase	increase	negligible change*
Energy maximizer	decrease	decrease	increase	decrease

NOTE.—These changes are illustrated in fig. 3.
*See text for explanation.

basically time minimizers or energy maximizers, and whether or not they satisfy the basic assumptions of the model. Following controlled experimental manipulations of food production or density and competitor density, changes in territory size and time budgeting can be documented and compared with the results predicted in table 1. Note that any such experimental observations must occur over a long enough period that a new equilibrium in the test animal's energy-time budget can be established. Otherwise, the short-term response of the animal to such manipulations would not provide a realistic test of the model.

A portion of table 1 requires further explanation. It is assumed that the daily net energy requirement ΔE (and thus ΔT) is relatively fixed for time minimizers, regardless of any changes in time budgeting. This assumption requires some justification. Note in figure 3 that the predicted changes in territory size should alter the amount of available "sitting" time (T_s), which may in turn alter the required ΔE (and thus ΔT). It is probable, however, that the amount of energy required for sitting is negligible compared to the amounts involved while foraging or chasing intruders. Therefore, the effect of variations in territory size upon ΔE , and thus ΔT , is listed in table 1 as a "negligible change."

Empirically, the only nonbreeding feeding territorial animals for which detailed time and energy budgets have been published are certain hummingbirds (e.g., Pearson 1954; Stiles 1971; Wolf and Hainsworth 1971) and ecologically equivalent sunbirds (Gill and Wolf 1975; Pyke 1979) and honeycreepers (Carpenter and MacMillen (1976a). Male hummingbirds (*Calypte anna*, *Eulampis jugularis*) and sunbirds (*Nectarinia reichenowi*) appear to function mainly as feeding-time minimizers, since each animal apparently defends a nearly fixed number of nectar-producing flowers, spending a large portion of the day sitting. There is also little variation in the budgeting of time and energy between individuals. Honeycreepers (*Vestiaria coccinea*), on the other hand, more closely resemble food-energy maximizers, in that they spend relatively large portions of the day feeding and little time sitting. (See Wolf et al. 1975 for a discussion of nectar-feeding bird energy-time budgets in terms of foraging efficiencies.)

Field observations indicate that nectar-feeding birds generally exhibit an inverse correlation between territory size and food production (Wolf 1969; Gill and Wolf 1975; Carpenter and MacMillen 1976a; Gass et al. 1976; Lyon 1976; Kodric-Brown and Brown 1978; Gass 1979), although little is known of the behavioral mechanisms involved. For example, Ewald and Carpenter (1978) found that when the availability of artificial food sources is experimentally decreased, male hummingbirds may spend progressively less time on their territories and defend them less vigorously rather than adjust territory size. Carpenter and MacMillen (1976b), on the other hand, found that the fewer the number of included flowers (above some lower threshold), the more vigorously honeycreepers will defend their territories.

Thus, few experimental field data presently exist to evaluate the above predictions, none of which include the necessary time budget analyses. Indeed, the effect of controlled variations in nonterritorial competitor density upon territory size has yet to be quantitatively investigated. The prediction that territory size should vary inversely with available food production, however, has been

demonstrated by controlled experimentation for the limpet *Lottia gigantea* (Stimson 1973), the freshwater fish *Salmo gairdneri* (Slaney and Northcote 1974), the tropical reef fish *Pomacentrus jenkinsi* (Syrop 1974), the temperate reef fish *Embiotoca jacksoni* (Hixon 1979), and the lizard *Sceloporus jarrovi* (Simon 1975). Likewise, the territories of red grouse (*Lagopus scoticus*) contracted after artificial improvement of their food, although a time lag indicated that the results were indirect (Miller et al. 1970).

Nonexperimentally, an inverse correlation between territory size and food availability has been observed or inferred for fishes (Clarke 1970; Larson 1977; Thresher 1977; Tanaka 1980; but see Symons 1971), many birds (Kluyver and Tinbergen 1953; Lockie 1955; Pitelka et al. 1955; Gibb 1956; Stenger 1958; Moss 1969; Holmes 1970; Maher 1970; Carl 1971; Cody and Cody 1972; Eltringham 1975; Newton et al. 1977; Salomonson and Balda 1977; Lance 1978; Miller and Watson 1978; but see Erickson 1938; Krebs 1971; Zach and Falls 1979), and certain mammals (Koford 1957; Smith 1968; but see Kemp and Keith 1970). However, since many of the bird species mentioned here are territorial only during the breeding season, the current model may not be strictly applicable.

At any rate, simple qualitative agreement between these data and the above predictions does not constitute a legitimate test of the model. The suggested experimental analyses of the time budgets of territorial animals should eventually provide such a test. The added effects of successful intruders, contiguous territories, and reproductive activities upon territory size will now be discussed in greater detail.

THE EFFECTS OF SUCCESSFUL INTRUDERS

Until now, I have assumed that the occupant is entirely successful in expelling all foraging intruders from the territory. In reality it seems that the larger the territory, the greater the probability will be that any given intruder will be able to consume some food before being chased. For solitary intruders, this effect would probably be minor and not alter the above predictions, since the occupant could chase each intruder before it consumed a significant amount of food.

As indicated by Brown and Orians (1970), however, behaviorally and/or morphologically divergent heterospecific intruders might be extremely difficult to efficiently expel from the territory. Examples occur among tropical reef fishes. By forming dense schools, various grazing species successfully invade and forage within the territories of surgeonfishes (Barlow 1974a) and damselfishes (Syrop 1974; Robertson et al. 1976). Such competitors are thus able to decrease the availability of food within the territory. Under these circumstances the occupant can successfully maintain a territory only by restricting its foraging to those microhabitats that cannot be overexploited by the heterospecific intruders. Qualitatively, this results in the same effect as decreased food production: The optimal territory size of both time minimizers and energy maximizers becomes larger than if no heterospecific competitors were present.

This effect has been documented for the damselfish *Pomacentrus jenkinsi* by

Syrop (1974). A comparison of patch reefs located within the same general habitat, but spatially isolated, revealed a positive correlation between territory size and relative density of various schooling grazers. A similar phenomenon may occur among song sparrows (*Melospiza melodia*). Yeaton and Cody (1974) found a strong positive correlation between territory size and the number of potential competitor species present. Unfortunately, the population density of each competitor species was apparently not measured.

THE EFFECTS OF TERRITORY CONTIGUITY

As the density of feeding territorial individuals increases, a point will be reached in a uniform environment where the optimally-sized territories become contiguous. Further increases in density can occur only with territory compression below the otherwise optimum size, with the territory borders often forming a mosaic of polygons (Grant 1968; Barlow 1974*b*).

The idea that at least some of the territories in a contiguous mosaic are compressed below the otherwise optimal size has been demonstrated in studies where territory occupants have been experimentally removed or have naturally disappeared. Following such disturbances, the former neighbors of the removed individuals almost invariably expand their territories until the empty space is reoccupied, or until their territories reach the presumably noncontiguous optimal sizes. This effect has been observed in fishes (Sale 1974, 1975; Nursall 1977) and birds (Thomas 1946; Lanyon 1956; Willis 1960; Jenkins et al. 1963; Krebs 1971; Welsh 1975; but see Dixon 1956). Additional data indicate that differential social dominance between neighbors is the source of territorial compression under contiguous conditions for fishes (Morris 1958; Assem 1967; Constanz 1975) and birds (Tompa 1962; Choate 1963; Watson 1964; Watson and Miller 1971). In these studies the most aggressive individuals possessed the largest (presumably near optimally-sized) territories.

Thus, where territories form a contiguous mosaic, certain individuals may possess territories which are smaller than the noncontiguous optimum. Varying food production should influence such compressed territories only when the ideal noncontiguous optimal size (\hat{r}) becomes smaller than the actual compressed size (r_{comp}). Thus, with increasing food production, compressed feeding territories of both time minimizers and energy maximizers should initially remain stable in size, then rather abruptly become progressively smaller (fig. 4). At this point the territories would no longer be contiguous, unless newly territorial animals settled, eventually establishing a new contiguous equilibrium. This effect has not yet been demonstrated, but it suggests that food availability may be a primary factor responsible for the inverse relationship between contiguous territory size and population density observed in fishes (Clarke 1970; Kodric-Brown 1977, 1978), many birds (Huxley 1934; Kendeigh 1941; Conder 1956; Durango 1956; Johnston 1956; Pitelka 1959; Watson 1965; Weedon 1965; Schartz and Zimmerman 1971; Zimmerman 1971; Harmeson 1974; Morse 1976; Vines 1979; but see Nice 1937) and a mammal (Armitage 1974).

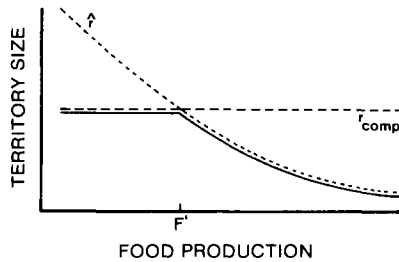


FIG. 4.—The effect of changes in food production upon territory size where the occupant has been forced to contract its territory to some size (r_{comp}) below the noncontiguous optimum (\hat{r}) due to interactions with contiguously territorial neighbors. Below some level of production (F'), the ideal \hat{r} is larger than r_{comp} , and so the territory remains at the compressed size. Above F' , however, \hat{r} becomes smaller than r_{comp} would have been, and so increased production results in decreased territory size. Thus, with increasing food production, contiguous territories should initially remain stable in size, then rather abruptly become progressively smaller. This effect is represented by the solid line. See text.

THE EFFECTS OF REPRODUCTIVE ACTIVITIES

During the breeding season, the adaptiveness of territoriality obviously shifts from augmenting future reproductive potential to enhancing immediate reproductive success. Territory size among the most intensively studied of all territorial animals, the birds, may remain stable throughout the breeding season (review by Schoener 1968), or fluctuate tremendously (Stenger and Falls 1959; Stefanski 1967; Root 1969; Yarrow 1970). Apparently the factors controlling territory size during the reproductive period vary among species exhibiting different mating systems and within species occupying different habitats (review by Welty 1975; see also Verner and Willson 1966; Orians 1969; Jenni 1974; Wittenberger 1976; Altmann et al. 1977; Emlen and Oring 1977). Additionally, in species that are territorial only during the breeding season, territory sizes may differ if the animals settle sequentially rather than simultaneously (Assem 1967; Knapton and Krebs 1974; see also Maynard Smith 1974).

Rather than attempting a detailed presentation of the confounding effects of reproductive activities upon feeding territory size, therefore, only some general ideas will be discussed.

As a result of sexual selection (see O'Donald 1963; Williams 1966; Trivers 1972), as well as simple spatial considerations, the territorial sex (usually the male) may defend as large an area as possible at the beginning of the breeding season. Indeed, a positive correlation between male territory size and the number of attracted females has been noted in some fishes (Assem 1967; Constanz 1975) and a lizard (Trivers 1976). In birds, territory size and/or the amount of food within the territory may constitute the basis of female choice (Verner 1964; Verner and Engelson 1970; Wolf and Stiles 1970; Ralph and Pearson 1971; McLaren 1972; Potter 1972; Best 1977).

The existence of such "area maximizers" (or simply "misers") can be readily accommodated by the current model. Assuming such males are feeding-time minimizers, they would simply defend the largest possible area that provided some

fixed daily energy requirement (ΔE_{fix}). The optimal territory size for an area maximizer is thus illustrated in figure 2 as \hat{r}_A . Note that "spare" food energy is contained within the territory each day, depicted as E_s in figure 2B. In addition to immediate reproductive benefits, Verner (1977) suggested that an area maximizer may inhibit the reproductive performance of other animals by preventing them from utilizing the spare food within its "super-territory," thus increasing the territory occupant's relative fitness (but see Rothstein 1979; Tullock 1979).

(Under certain circumstances, nonbreeding animals may also function as area maximizers [Lockie 1966; Myers et al. 1979]. Note that the optimal territory size of such animals should not be affected by changes in food production, but should vary inversely with competitor density [fig. 3]. Where food production and competitor density increase concurrently, therefore, territory size of area maximizers should decrease. Data supporting this prediction have been provided recently for both breeding [Seastedt and MacLean 1979] and nonbreeding birds [Myers et al. 1979].)

Once a mate has been attracted, the territorial individual must obviously devote time and energy to any subsequent reproductive activities. Where territories are noncontiguous, this should result in territorial contraction below the optimal size for an area maximizer. (Qualitatively, this limitation in time is identical to decreasing T_{tot} in fig. 2.) Where territories are contiguous, however, territory size may possibly remain stable due to habituation and the resulting decrease in agonistic behavior between neighbors. Such habituation has been noted in fishes (Assem and Molen 1969; Peeke 1969; Peeke and Peeke 1970; Peeke et al. 1971; Baylis 1974) and birds (Weedon and Falls 1959; Falls 1969; Krebs 1971).

If parental care of the offspring is required, the optimal territory size becomes a compromise between maximizing the amount of food available to the young by defending as large an area as possible, and allowing sufficient time to feed and care for the young by defending a limited area (see Orians 1971).

Whatever the modifying effects of various mating systems and reproductive activities may be, therefore, the primary environmental determinants of feeding territory size should remain the same as those between breeding seasons: food production and competitor density.

SUMMARY

An energy-time budget model is developed which predicts the influence of various environmental factors upon feeding territory size. For nonbreeding animals maintaining noncontiguous territories, territory size should (1) vary inversely with food production, but directly with competitor density, for feeding-time minimizers (defined here as animals that exhibit relatively fixed daily energy requirements); and (2) vary inversely with both food production and competitor density for food-energy maximizers, animals whose potential reproductive success is positively correlated with their net energetic intake. Concomitant predicted changes in time budgeting provide operational criteria for testing the model.

Besides the primary effects of food and competitors, other factors may also influence territory size. Any competitors which successfully invade the territory

can decrease the availability of food, forcing both time minimizers and energy maximizers to expand their territories. Where territories are contiguous, differential social dominance between neighbors can force certain individuals to contract their territories below the otherwise optimal size.

Finally, sexual selection and other factors may result in males defending as large an area as possible. Whether between or during breeding seasons, territory size of such "area maximizers" should not be affected directly by changing food production, but should vary inversely with competitor density. As the breeding season progresses, subsequent reproductive activities may or may not result in territorial contraction, depending upon such factors as the degree of habituation between neighbors and the level of parental care.

Although some of the predictions of the model are qualitatively supported by field evidence, data necessary for adequate quantitative tests are presently unavailable. Suggested experimental investigations of the time budgets of territorial animals under controlled environmental conditions will undoubtedly provide major refinements and revisions of the tentative ideas presented here.

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APPENDIX A

SYMBOLS OF THE MODEL

- C = Number of nonterritorial competitors per unit area.
 ΔE = Net energy gain per day ($= E_f - E_c$); value may be fixed (ΔE_{fix}) or represent a maximum (ΔE_{max}).
 E_c = Energy consumed chasing nonterritorial competitors per day.
 E_f = Energy gained from territory food per day.
 $E_{f\text{max}}$ = Total available food energy produced within territory per day.
 E_s = Energy "saved" in territory food reserves per day.
 e = Energy consumed per unit chase distance.
 F = Daily available food biomass produced per unit area.
 f = Biomass of food consumed per unit foraging time.
 o = Percent dietary overlap between territory occupant and intruding competitor.
 r = Territory radius or its equivalent; mean chase distance per intruder.
 \hat{r}_A = Optimal territory size for an area maximizer.

- \hat{r}_E = Optimal territory size for an energy maximizer.
- \hat{r}_T = Optimal territory size for a time minimizer.
- r_{comp} = Compressed contiguous territory size.
- s = Mean speed of wandering nonterritorial competitor.
- ΔT = Time spent feeding relative to chasing (= $T_f - T_c$); value may be fixed (ΔT_{fix}) or represent a maximum (ΔT_{max}).
- T_c = Time spent chasing nonterritorial competitors per day.
- T_f = Time spent feeding per day; value may represent total time available for feeding (T_{af}) and/or time required to consume total food production of territory (T_{rf}).
- T_s = Total "spare" time available per day.
- T_{tot} = One daylight period.
- t = Time spent per unit chase distance.
- y = Net energy yield per unit biomass of food eaten.

APPENDIX B
DERIVATIONS OF \hat{r}_T AND \hat{r}_E

At the optimal territory size for the time minimizer (\hat{r}_T), the daily feeding time (T_f) equals the time required to consume the total daily food production (T_{rf} of eq. [3b]), as depicted in figures 1 and 2. Thus, equation (4b) becomes $\Delta T_{fix} = T_{rf} - T_c$. Inserting equations (3b) and (2a),

$$\Delta T_{fix} = \frac{\pi \hat{r}_T^2 F}{f} - 2 \hat{r}_T^2 t T_{tot} \sum_{i=1}^n (sCo)_i.$$

Therefore,

$$\hat{r}_T = \left[\frac{\Delta T_{fix}}{(\pi F/f) - 2t T_{tot} \sum_{i=1}^n (sCo)_i} \right]^{1/2},$$

which is equation (5). The optimal territory size for the energy maximizer occurs at the single radius (\hat{r}_E) where $T_f + T_c = T_{tot}$ and $T_f = T_{rf}$ (see figs. 1 and 2). Thus, inserting equations (3b) and (2a) into equation (1),

$$T_{tot} = \frac{\pi \hat{r}_E^2 F}{f} + 2 \hat{r}_E^2 t T_{tot} \sum_{i=1}^n (sCo)_i.$$

Therefore,

$$\hat{r}_E = \left[\frac{T_{tot}}{(\pi F/f) + 2t T_{tot} \sum_{i=1}^n (sCo)_i} \right]^{1/2},$$

equation (6).

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